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GEO-PRESENTATION AND GEO-REACTION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 268

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(WITH FIVE FIGURES)

Historical

The reaction of plants to geotropic stimulation has been the subject of considerable investigation, the problem having been attacked from many standpoints. Naturally, perhaps, the physical side was studied first, a number of workers having developed the main features of gravity stimulus, presentation and reaction times, perception, conduction and response, organs of perception, and other related subjects. The chemical side of the field, involving the change in metabolism of the stimulated organ, has received much less attention.

The first worker in this field seems to have been KRAUS. As early as 1870 he published (**14**) the first of a series of researches on the chemical content of the growing plant, both in normal relations and after subjection to various external stimuli. This research included (1) the water content, (2) the acidity, (3) the sugar content of the normally growing shoot, (4) the relation of each to the growth maximum, and (5) steps in the change of the cell content of the concave and convex side of the geotropically and heliotropically responding organ. He determined that, in the normally growing shoot, (1) the acidity decreases from the tip downward, (2) the water increases relatively from the tip to the downward limit of growth, and (3) the sugar increases from the tip below the growth maximum and therefore is not a limiting factor in growth. In the stimulated organ he found on the convex-becoming side (1) an increase of sugar production up to the time of visible curvature and then a decrease, (2) a progressive decrease in acidity during stimulation, free acid being entirely absent from the responded organ, and (3) a progressive increase of water preceding curvature.

DEVRIES (5) studied the forces released in gravity stimulus, the effect of these released forces upon curvature, and the release of elasticity by gravity stimulus. He concludes that gravity produces an increase of osmotically active material in the cells of the convex-becoming side, causing an intake of water from the adjacent tissue, the resulting increased turgor producing a longitudinal extension of the elastic cell membranes, which, originally plastic, become fixed through growth and lignification.

CIELSIELSKI (2) observed a difference of the cell sap on opposite sides of geotropically stimulated roots, the cells of the convex-becoming flank exhibiting a thin watery protoplasm in contrast with the denser, more opaque plasma of the side becoming concave. KOHL (13) obtained analogous results in the sporangiophores of *Phycomyces*, in that in geotropic stimulation the plasma of the concave side of the filament became much thicker, while that of the convex side became thin and watery. He concluded that there was a causal relation between this differentiation of cell plasma and the curvature of the organ. ELFVING (7), however, according to his reviewers, produced a similar differentiation of protoplasm in *Phycomyces* sporangiophores by allowing them to push against a glass obstruction, a purely mechanical stimulation.

HILBERG (11), contrary to DEVRIES' results, found that in geotropic stimulation the osmotic pressure of the concave side of leaf joints and stem nodes of various plants is greater than that of the convex side. WORTMAN (22) negatives both DEVRIES' and HILBERG'S conclusions, since he could find no difference in the osmotic pressure of the two flanks of stimulated organs, and holds DEVRIES' view of the causal relation between turgor and curvature to be wholly untenable. On the other hand, he agrees with KOHL in that he found in geotropically stimulated organs the plasma "wandered" from the convex to the concave side, the thickened plasma inducing the cell membranes of the concave side to become thicker but less elastic and less extensible than those of the convex side. These latter, stretching longitudinally, force the concave side upward, thus producing curvature. NOLL (16) confirms WORTMAN'S work, but refutes his argument of the causal relation between the changed activity of the plasma and the curvature of the organ.

COPELAND (3) was unable to detect a difference in the opposite flanks of stems split lengthwise and stimulated geotropically four days. KERSTAN (12), using the plasmolysis method, found no increase of turgor in either flank of geotropically or heliotropically stimulated shoots either during curvature or after its completion. He concludes with NOLL that the decrease of turgor is due to the fact that the osmotic producing substances do not keep pace with the intake of water of the cells and their increased volume.

THATE (20) found KRAUS's method too crude to determine the difference of water in the two flanks of heliotropically stimulated shoots, although he does not dispute its existence. On the other hand, TONDERA (21) was able to verify KRAUS on this point and from his studies developed the law: "As the cells of the rind parenchyma of the lower organ half become filled by the streaming of water, due to gravity, the cells of the opposite half become water-poor, the resulting difference in pressure forcing the organ to move toward the water-poor half." This at best is a very crude conception.

From the cytological standpoint, McDOUGAL (15) found that the cells of the convex side are greater in length, breadth, and thickness than those of the corresponding tissue of the concave side of geotropically stimulated roots. GEORGEVITCH (8) confirms this earlier work, while BÜCHNER (1) found the same condition in shoots that had been prevented from responding to gravity stimulation.

CZAPEK (4) is probably the chief worker in the chemical field of geo-presentation and reaction. Working with normal seedlings, he found that homogentisic acid is produced as a product of the oxidation of tyrosin, through the action of an oxidase, tyrosinase. In geotropic stimulation the tyrosin is converted into homogentisic acid by tyrosinase, as in normal seedlings, but the further oxidation of the homogentisic acid by the oxidase is inhibited by the production of an anti-oxidase, which renders the oxidase partly ineffective and by this means causes an accumulation of homogentisic acid. The accumulation begins after five minutes' stimulation, reaches a maximum at the time of distinct curvature, and disappears when reaction is complete. GROTTIAN (10) and GRAFE and LINSBAUER (9), however, were unable to confirm his results. They found as great variation in the amount of homogentisic acid in different analyses of normal shoots as CZAPEK found between the stimulated and unstimulated organs.

In her work on thermotropism of roots, ECKERSON (6) found the greater permeability to be on the concave side of the root, and that this permeability changed with the changed thermotropic reaction of the root.

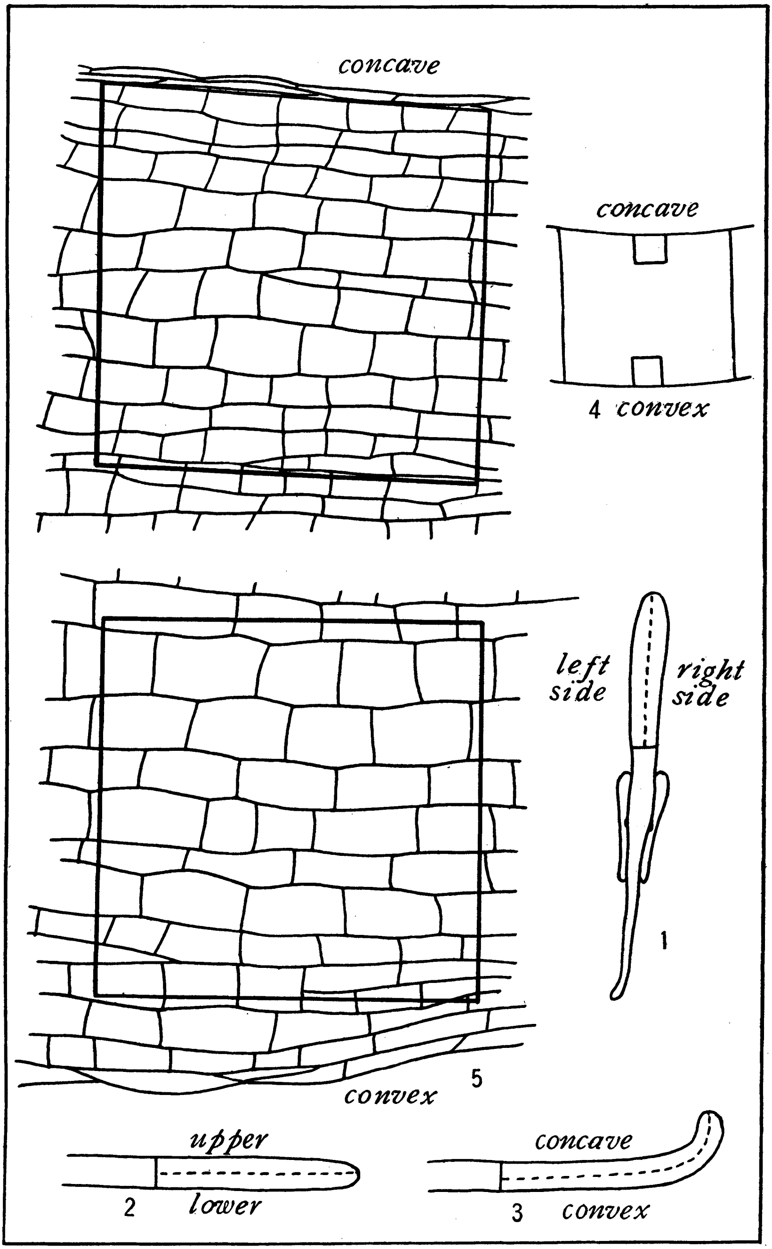
Scope of experiment

The work here presented is a continuation of that reported in a previous paper (18), which dealt with the acidity of the normal shoot, and compared the acidity of the two flanks of the geotropically stimulated shoot. The present paper deals with the changes in metabolism of the carbohydrates, the difference in osmotic pressure, and the difference in respiration of the upper and lower flanks of the geotropically stimulated shoot through presentation and reaction periods. *Vicia Faba* seedlings were employed throughout the experiment because they respond readily to geotropic stimulation, and because they are large enough to be easily split longitudinally. Trouble was experienced in germinating the seeds because of the development of mold. To overcome the difficulty the seeds were washed in tap water and then soaked two or three minutes in a 1 per cent solution of silver nitrate and rinsed thoroughly. They were grown in sand which had been sterilized by boiling in water an hour or longer, and then put into sterile pots while hot and allowed to stand until the following day before planting the seeds.

Carbohydrates and proteins

For this analysis etiolated seedlings of *Vicia Faba*, grown in sand in the greenhouse at a temperature of about 20° C., were used. When the seedlings were 6–8 cm. high they were geotropically stimulated for periods ranging from 15 minutes to 5 hours. Duplicate analyses of samples for each period of stimulation, as well as duplicate analyses of the unstimulated organ as controls, were made.

The epicotyls were split longitudinally into right and left halves (fig. 1) in the controls, and into upper and lower halves


concave
concave
4 convex
left side
right side
1
5
convex
upper
2 lower
concave
3 convex

FIGS. 1–5

(fig. 2) in the stimulated seedlings. These latter become the concave and convex halves (fig. 3) respectively in the responded organ. Samples varying from 6 to 10 gm. were used. The fresh portions were weighed in weighing bottles and the weight obtained by difference. The tissue, thus obtained, was cut up fine and triturated, killed in boiling 85 per cent alcohol, and boiled for 30 minutes.

The triturated tissue was subjected to alcoholic extraction for 3 hours and to ether extraction for 2 hours in the Koch modification of the Soxlet extractor. The tissue was then pulverized and extracted in boiling water 30 minutes. This water extraction was repeated six times. Following this was another alcohol extraction of 24 hours. The original killing alcohol, the ether extract (the ether was evaporated and the extract brought into solution in water), the water extract, and the two alcohol extracts were combined, and the volume increased to 500 cc. by the addition of water. This extract contained all the material soluble in these solvents, that is, the sugars, the lipoids, and the amino acids, and may be designated F_1. The residue contained the insoluble substances (starches, pectins, hemicelluloses, and cellulose), and may be designated F_2. From F_1 was taken three 150 cc. portions for the determination of (1) sugar, (2) nitrogen, and (3) dry weight. From F_2 was obtained (1) the dry weight and (2) the hydrolyzable polysaccharides.

The alcohol-water-soluble portion for the determination of sugar was freed from alcohol by evaporation on the steam bath, water being added before and during the process of evaporation, and the final volume brought to 150 cc. The tannins and lipoids were precipitated by the addition of a 10 per cent solution of basic lead acetate, the volume made up to 200 cc. and filtered immediately. The excess lead was precipitated from 150 cc. of the filtered solution by means of a saturated solution of ammonium sulphate, and the volume brought again to 200 cc. Duplicate determinations of 50 cc. portions were made of sugar solutions thus obtained, by the Munson and Walker method for the determination of reducing sugars (17). The amount of cuprous oxide thus obtained was determined by the volumetric potassium permanganate method (*op. cit.*, pp. 52, 53.). An N/20 solution of permanganate was used. A third 50 cc. portion of this clarified solution was used for the determination of non-reducing or hydrolyzable sugars. The hydrolysis was performed according to the method for the determination of sucrose in the absence of raffinose (*op. cit.*, pp. 40, 41). The cooled solution was neutralized with 20 per cent sodium hydrate, brought to 100 cc. volume, and duplicate sugar estimations made of 50 cc. portions as described.

The residue (F_2), after the determination of the dry weight (to be described later), was used for the determination of the polysaccharides according to the method for direct acid hydrolysis of starch (*op. cit.*, p. 53). Duplicate determinations of 50 cc. portions were used for the determination of sugars, as in F_1.

The calculations were based on the milligrams of copper oxidized in the change from cuprous to cupric oxide, and expressed in equivalent milligrams of dextrose obtained from the Munson and Walker table accompanying the method of analysis (p. 243).

The portion of F_1 for the determination of dry weight was evaporated to moist dryness on the steam bath and brought to constant weight in vacuo. The dry weight of F_2 was obtained by bringing the residue of the original tissue to constant weight in the electric oven at a temperature of 104° C. The calculations for both were based on the dry weight per gram of the fresh material.

The third portion of F_1 was used for the determination of the total nitrogen. This determination was made after the Kjeldahl method as modified by ARNOLD. Calculations were made on the amount of nitrogen per gram of fresh weight. Table I shows the results obtained. It will be noticed that the soluble sugars vary but little throughout. The hydrolyzable sugars increase markedly at the time of visible response, and are greater on the convex side. The polysaccharides decrease as the hydrolyzable sugars increase. The dry weight of F_1 remains practically constant. The dry weight of F_2 remains practically constant until the beginning of curvature, when the weight of the convex side becomes less. The results of this sugar determination are not comparable with the work of KRAUS, for he was working with the raw pressed sap, which probably contained reducing substances other than sugars, as he himself suggests.

Kraus found that the reducing substances increased on the convex side of the responding organ up to the time of visible curvature, and then decreased on that side of the curved shoot, a point upon which he has frequently been misquoted (**14**, pp. 87 and 89). The total nitrogen remains constant throughout, the unstimulated sample I showing almost identically the value of sample IX at the close of the experiment.

TABLE I

DETERMINATION OF MATERIAL PER GRAM FRESH WEIGHT

TIME STIMULATED	F_1	F_1	F_2	F_1	F_1	F_2	F_1
	Soluble sugar (mg.)	Hydrolyzable sugar (mg.)	Polysaccharide (mg.)	Total carbohydrates (mg.)	Dry weight (g.)	Dry weight (g.)	Total nitrogen (g.)
Sample I, unstimulated							
8.74 (right)	23.45	3.21	3.60	30.26	0.06845	0.01920	0.004800
9.35 (left)	23.30	3.95	3.31	30.56	0.06878	0.01876	0.004535
Sample II, stimulated 15 min.							
11.88 (upper)	23.58	2.96	5.75	32.29	0.07124	0.02449	Lost
12.05 (lower)	22.20	3.10	4.93	30.23	0.06894	0.02176	Lost
Sample III, stimulated 30 min.							
10.38 (upper)	19.45	3.54	3.37	26.36	0.06460	0.01809	Lost
10.38 (lower)	19.35	3.58	3.02	25.95	0.06888	0.01887	Lost
Sample IV, stimulated 1 hour							
11.58 (upper)	22.44	4.94	4.00	31.38	0.06296	0.01994	0.004346
12.20 (lower)	22.00	4.73	2.98	29.71	0.06621	0.02014	0.004353
Sample V, stimulated 1.5 hours							
7.17 (upper)	21.90	6.34	4.72	32.96	0.05788	0.02224	0.004238
7.09 (lower)	21.62	4.82	4.66	31.10	0.06379	0.02146	0.004448
	Beginning visible response						
Sample VI, stimulated 2 hours							
10.23 (upper)	18.65	6.20	2.44	27.29	0.05803	0.01828	0.003697
10.15 (lower)	21.50	9.15	3.66	34.31	0.06318	0.01832	0.003838
Sample VII, stimulated 3 hours							
9.32 (upper)	23.10	8.34	3.29	34.73	0.06716	0.02054	0.004421
9.05 (lower)	28.25	9.10	3.50	40.85	0.06802	0.01950	0.004738
Sample VIII, stimulated 4 hours							
9.69 (upper)	23.05	4.96	3.44	31.39	0.07426	0.02100	0.003985
9.66 (lower)	23.45	7.86	3.18	34.49	Lost	0.01875	0.004144
Sample IX, stimulated 5 hours							
6.92 (upper)	21.10	9.20	1.88	32.18	0.06713	0.01907	0.004855
7.63 (lower)	26.75	13.82	2.62	43.19	0.06783	0.01686	0.004593

Osmotic pressure

The osmotic pressure of the two flanks during the period of presentation and response was determined by means of plasmolysis. Weight molecular solutions of cane sugar and potassium nitrate were used as plasmolyzing agents. The seedlings were geotropically stimulated for varying periods of time. Portions of the seedlings, including the region of response, were sectioned (on the hand microtome) vertically, that is, from upper to lower side of the horizontally placed shoot. The sections were placed in weight molecular solutions of the plasmolyzing agent of such percentages as previous experiment had shown to be close to the plasmolyzing point. The series of weight molecular solutions was graduated to intervals of one-half of 1 per cent. The accompanying tables and graphs show the results of one each of the experiments made.

PLASMOLYSIS

(Using cane sugar as plasmolyzing agent)

In normal shoots both sides plasmolyze at 42 per cent weight molecular
After 5 minutes' stimulation both sides plasmolyze at 42 per cent
After 10 minutes' stimulation both sides plasmolyze at 43 per cent
After 45 minutes' stimulation upper side at 43, lower side at 44 per cent
After 1.5 hours' stimulation upper side at 43, lower side at 44.5 per cent
After 5 hours' stimulation both sides at 43 per cent

(Using potassium nitrate as plasmolyzing agent)

In normal shoots both sides plasmolyze at 31 per cent weight molecular
Stimulated 15 minutes both sides plasmolyze at 31 per cent
Stimulated 30 minutes both sides plasmolyze at 32 per cent, upper general, lower a few cells
Stimulated 45 minutes upper faintly at 33, lower at 33.5 per cent
Stimulated 1.25 hours upper at 32, lower at 33 per cent
Stimulated 5 hours both sides at 32 per cent

These results indicate that the osmotic pressure of the cell rises as the time of stimulation increases, reaches a maximum at or before visible response, and decreases as the response nears completion. The osmotic pressure is greater on the convex side during the period of response. It is interesting to note that the maximum acidity, as shown in a previous paper (18), is reached in 30 minutes, while the maximum turgor is reached in 45 minutes. The results of different investigators on the turgor change of stimulated shoots show little agreement. Some writers have found the greater turgor on the concave, some on the convex, side; others have found no difference in turgor in either flank of the stimulated shoot or in the stimulated versus the unstimulated organ, with the balance of the argument rather in favor of the last mentioned. Inspection of the work of those writers who have tabulated their results, however, shows that the time of stimulation (ranging in general from several hours to several days) was too long to catch the change in turgor, which change appears to take place in a relatively short time, as was originally determined by DEVRIES in his macroscopic turgor experiments on geotropically stimulated grass nodes.

Respiration

Qualitative experiments were conducted upon the relative respiration of stimulated and unstimulated roots, and upon the upper and under flanks of geotropically stimulated shoots. These experiments were made in the TASHIRO (19) biometer apparatus, which determines the relative rate of respiration by the precipitation of barium carbonate on the surface of a drop of barium hydrate in a closed chamber.

The roots, without previous stimulation, were placed, one horizontally and one vertically, in similar chambers designated as left and right respectively. The shoots were stimulated for periods varying from 10 minutes to 5 hours. They were split longitudinally just before being placed in the apparatus. The roots were suspended and the shoots were placed horizontally, the upper with the cut surface down, and the lower with the cut surface up, as during stimulation. Both were placed across Van Tieghem cells in order to give equal opportunity for carbon dioxide diffusion. Many seedlings were tested with uniform results.

Table II shows that a geotropically stimulated root has a higher rate of respiration than the unstimulated root, and that in the stimulated shoot the under (convex) side shows a higher rate of respiration than the upper (concave) side at all intervals of time during stimulation and response that were investigated. It also shows that the rate of respiration decreases as the time of stimulation increases.

The effect of geotropic stimulation upon the cell structure of the responded shoot was determined through microscopical examination. Longitudinal sections from concave to convex side of the completely responded shoot in the region of the angle of greatest curvature were cut on the freezing microtome, and camera lucida drawings were made of corresponding areas on the concave and convex flanks of the organ (figs. 4, 5).

TABLE II

RELATIVE RESPIRATION

Seedling	Left chamber	Right chamber	Time stimulated	Time in apparatus	Greater precipitation of $BaCO_3$
Roots					
Sunflower...	Horizontally placed	Vertically placed	....	4 minutes	Horizontal root
Sunflower...	Vertically placed	Horizontally placed	....	4 minutes	Horizontal root
Zea Mays...	Horizontally placed	Vertically placed	....	4 minutes	Horizontal root
Shoots					
Vicia Faba..	Convex side	Concave side	10 minutes	2 minutes	Convex (much greater)
Vicia Faba..	Convex side	Concave side	2 hours, 31 minutes	3 minutes	Convex side
Vicia Faba..	Concave side	Convex side	4 hours, 58 minutes	7 minutes	Convex side

A study of fig. 5 shows that the cells on the convex side are larger than those on the concave side. A 10 cm. square on the convex side contains 40 cells, while a corresponding area on the concave side shows 72 cells. This result is in accord with the work of previous investigators.

Summary

1. The reducing sugars remain constant throughout stimulation and response.
2. The hydrolyzable sugars increase on the convex side at the expense of the polysaccharides as response takes place.
3. The total sugars are constant until beginning of response, when the sugars of the convex side become greater.
4. The osmotic pressure increases until visible curvature has taken place. At the end of the reaction both flanks show the same osmotic pressure, which, however, is greater than that of the normal shoot.
5. Respiration of the geotropically stimulated root is greater than that of the unstimulated organ.

6. The rate of respiration of the convex side of the geotropically stimulated shoot is greater than that of the concave side throughout the period of perception and response.

7. Respiration decreases as the time of stimulation increases.

8. The steps, in point of time, of the chemical changes that take place in a geotropically stimulated shoot are: (1) increased respiration, (2) increased acidity (**18**), (3) increased turgor, and (4) increased production of hydrolyzable sugars with corresponding decrease of polysaccharides on the convex side of the responding organ.

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